

A TRIASSIC MYGALOMORPH SPIDER FROM THE NORTHERN VOSGES, FRANCE

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ABSTRACT. The oldest fossil mygalomorph spider, from the Anisian Grès à Voltzia of the northern Vosges, France, is described as *Rosamygale grauvogetti* gen. et sp. nov. The spider exhibits mainly plesiomorphic characters. It is a tuberculote (*sensu* Raven 1985) and is placed in the Hexathelidae, with some reservations. A ground-dwelling spider, *Rosamygale* was an integral part of the halophilous terrestrial biota of the time. The spiders became entombed in the wet sediment of desiccating pools. The presence of a primitive tuberculote on the southern margins of the Zechstein Sea in the Middle Triassic is evidence for a pan-Pangaean distribution of the Mygalomorphae prior to the break-up of the supercontinent.

RÉSUMÉ. La plus ancienne araignée mygalomorphe connue provient du Grès à Voltzia, d'âge Anisien, du Nord des Vosges (France). Elle est décrite sous le nom *Rosamygale grauvogetti* gen. et sp. nov. Cette araignée présente essentiellement des caractères plésiomorphes. Elle appartient aux formes 'tuberculote' (*sensu* Raven (1985)) et est rapportée avec réserve aux Hexathelidae. *Rosamygale* qui vivait au contact du sol, appartenait sans doute à la faune halophile de l'époque. Les araignées s'échouaient dans des étendues d'eau en voie d'assèchement et étaient enfouies dans le sédiment argileux. L'existence d'une forme primitive de 'tuberculote' durant le Trias moyen, sur la marge méridionale de la mer du Zechstein, apporte la preuve d'une distribution pan-pangéenne des Mygalomorphae antérieurement à la dislocation du supercontinent.

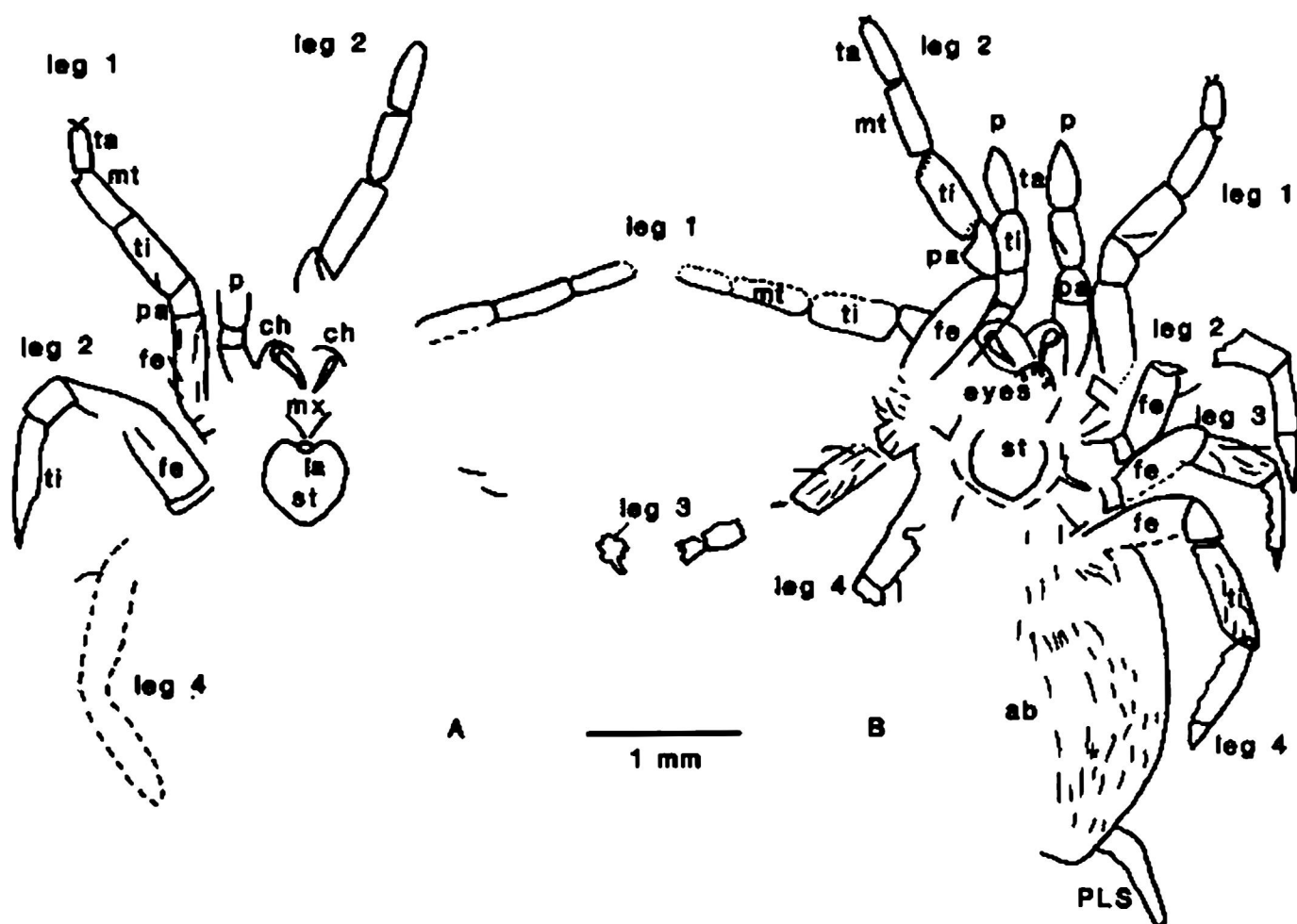
MYGALOMORPH spiders were first described from the Mesozoic by Eskov and Zonshtein (1990) from localities in the Lower Cretaceous of Transbaikalia and Mongolia. In addition, undescribed mygalomorphs are known from the Cretaceous of Brazil (N. Platnick, pers. comm.). Previously, only Cenozoic fossil mygalomorphs were known (reviewed in Eskov and Zonshtein 1990). Here, a new mygalomorph genus is described, exceptionally preserved in the middle Triassic (Anisian) Grès à Voltzia of the northern Vosges, and is placed in the extant family Hexathelidae. Thus, the fossil record of the Mygalomorphae is doubled, and it is suggested that the infraorder probably had a worldwide distribution before the break-up of the Pangaean supercontinent.

GEOLOGICAL SETTING

The sediments bearing the fossil spiders, the Grès à meules, form the lower part of the Grès à Voltzia, which belongs to the upper part of the Buntsandstein, of Lower Triassic (Anisian) age (Table 1).

Three facies have been recognized in the Grès à meules Formation (Gall 1971, 1983, 1985): (a) thick lenses of fine-grained sandstone, grey or pink but most often multicoloured, containing land plant debris and stegocephalian bone fragments; (b) green or red silt/clay lenses, generally composed of a succession of laminae each a few millimetres thick, with well-preserved fossils of aquatic and terrestrial organisms; (c) beds of calcareous sandstone with a sparse marine fauna.

The spiders come from the clay lenses (facies b); the associated fauna includes terrestrial scorpions, myriapods and insects. An aquatic fauna occurs in the same beds, represented by medusoids, annelids, *Lingula*, bivalves, limulids, crustaceans and fish. Land plants are also abundant, comprising horsetails, ferns, and gymnosperms (*Voltzia*). Some animals (e.g. *Lingula*, bivalves) are preserved in life position. Many arthropods (limulids, crustaceans) show, in the same horizon, different larval stages, adults, and moults. Insect egg-strings (Pl. 1, fig. 4), coprolites, and trace fossils are also present. The biota is rich in individuals but poor in species.

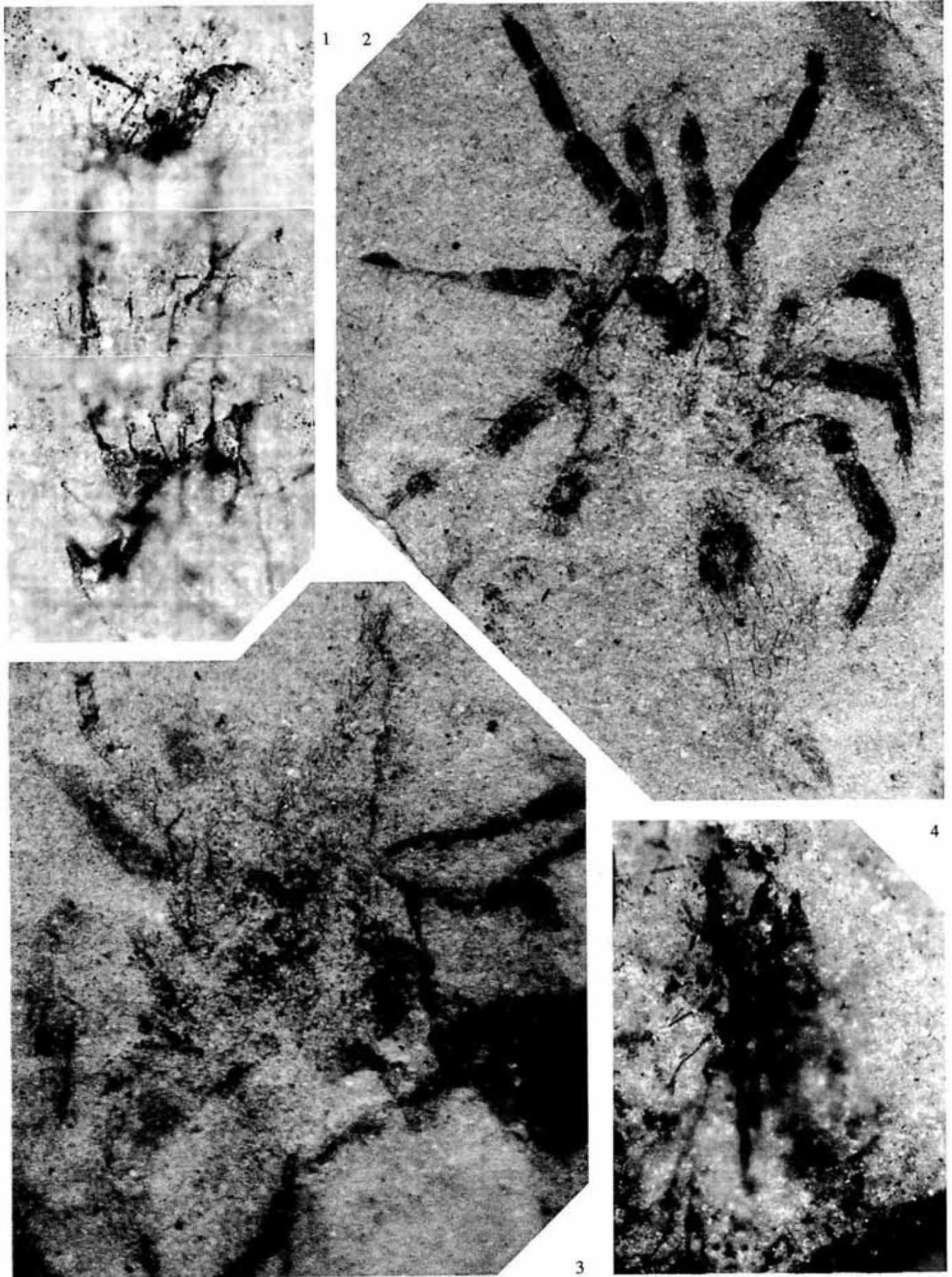


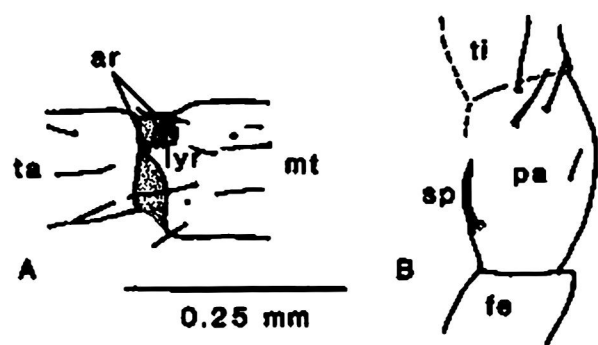
TEXT-FIG. 5. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR12; paratype, part; explanatory drawing for Pl. 4, fig. 3. B, AR12; paratype, counterpart; explanatory drawing for Pl. 4, fig. 2.

Land. Entrapment of wandering spiders in mud and mucilage is dependent on the habits of *Rosamygale*. During their lives (which may be a number of years for females, over 20 years in some species (Baerg and Peck 1970)), mygalomorphs leave the safety of the nest only for dispersal when young or, if male, to find a mate. Prey capture may involve a dash partly out of the nest; some species make radiating 'trip-lines', others arrange twigs in a radiating pattern from the nest entrance, the purse web of *Atypus* allows the capture of prey from entirely within the closed sac-like web, and other species lure prey inside the nest burrow (Main 1981, 1982, 1986; Coyle 1986). All of these strategies enable mygalomorph spiders to spend the least amount of time and distance outside the web. Therefore, it would normally either be during times of dispersal of young or adult male wandering that a mygalomorph spider would be likely to encounter a natural trap. Main

EXPLANATION OF PLATE 4

Figs 1-4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR12; counterpart; distal metatarsus and tarsus of left side of specimen (see fig. 3), note emarginated distal metatarsus with thorn (bottom left), pectinate paired claws (left one poorly preserved), and small median claw (below right paired claw), $\times 200$. 2, AR12; paratype, part; see Text-fig. 5B for explanation, $\times 22$. 3, AR12; paratype, counterpart; see Text-fig. 5A for explanation, $\times 22$. 4, AR5, counterpart, cheliceral fang, $\times 200$.





TEXT-FIG. 6. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR12; part; distal metatarsus and proximal tarsus of leg 2 of left side of specimen; explanatory drawing for Pl. 5, fig. 3. B, AR8; part; palp patella of left side; explanatory drawing for Pl. 4, fig. 3.

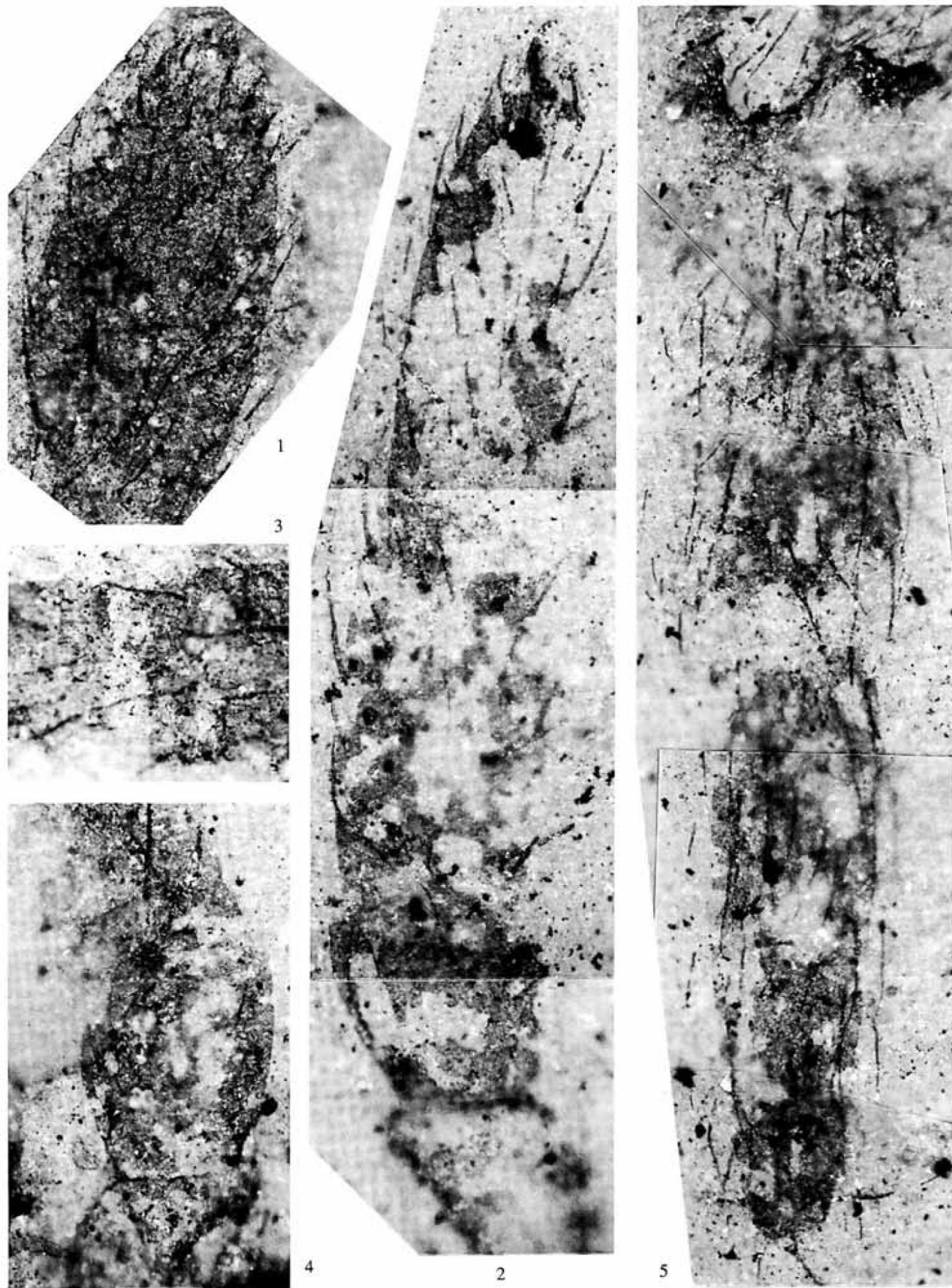
(1982) pointed out that most mygalomorphs adopt strategies for minimizing risk of predation and desiccation during these vulnerable periods. The timing of dispersal and wandering is closely linked with the rainy season: it is easier for the young to start constructing burrows in wet ground, and desiccation of spiders and eggs is avoided when reproduction takes place in humid conditions. Many arid habitat species aestivate, so male wandering must synchronize with female activity. Most Australian mygalomorphs disperse by running along the ground to the nearest suitable new nest site. Clustered populations occur in these species, which may be advantageous if the habitat is suitable (Main 1982). It is likely that male or immature specimens of *Rosamygale* were in the process of dispersal or wandering during a wet season or following rain when they became trapped in the desiccating pools. However, females living in an area which was inundated by standing water would eventually evacuate their tubes, might be unable to reach dry land, and could thus become trapped in the same manner.

Air. Floating on gossamer threads (ballooning) occurs among small araneomorph spiders (principally the erigonine linyphiids in the northern hemisphere), and is also practised by some mygalomorphs. Ballooning has advantages for dispersal in patchy or unstable environments. Mygalomorphs balloon by dangling from a twig on a silken thread until the wind breaks the thread and the spider takes to the air. In contrast, araneomorph ballooners may remain on the substrate, and spin special gossamer threads into the air until the air currents are sufficiently strong, when they let go (Coyle 1983, 1985). The mygalomorph method appears to be more primitive than that of the araneomorphs, since no special gossamer, only dragline silk, is used, and there is little control over the take-off in mygalomorphs (it simply occurs when the silk breaks). An evolutionary progression can be envisaged from dispersal by climbing up vegetation and dropping from draglines, through accidental windblown travel during drops ('rappelling'), to purposeful construction of ballooning platforms as observed in *Sphodros* by Coyle (1983). Coyle (1983) also reported that the mygalomorph ballooning method has been observed in some primitive araneomorphs. Silk has a high tensile strength (it does not break easily) so larger mygalomorphs would be at an advantage during take-off.

Since there was abundant vegetation surrounding the desiccating pools in which the Grès à Voltzia spiders became trapped, it is quite possible that they dropped or were blown from the

EXPLANATION OF PLATE 5

Figs 1–5. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR12; part; palp tarsus (see Pl. 4, fig. 2), $\times 200$. 2, AR8; part; palp of right side, distal femur to tarsus with single claw (see Pl. 2, fig. 2), $\times 200$. 3, AR12; part; distal metatarsus and proximal tarsus of leg 2 of left side of specimen (see Pl. 4, fig. 2), distal to left, superior to top, showing typical superior bicondylar hinge joint and lyriform; see Text-fig. 6A for explanation, $\times 200$. 4, AR8; part; palp patella of left side; see Text-fig. 6B for explanation, $\times 200$. 5, AR8; part; spinnerets of right of specimen (see Pl. 2, fig. 2), ALS (top right), PMS (top centre), and PLS; note distribution of spigots (setae with bulbous bases, see Pl. 6, fig. 4) especially at distal ends of spinnerets, lateral to right, $\times 200$.



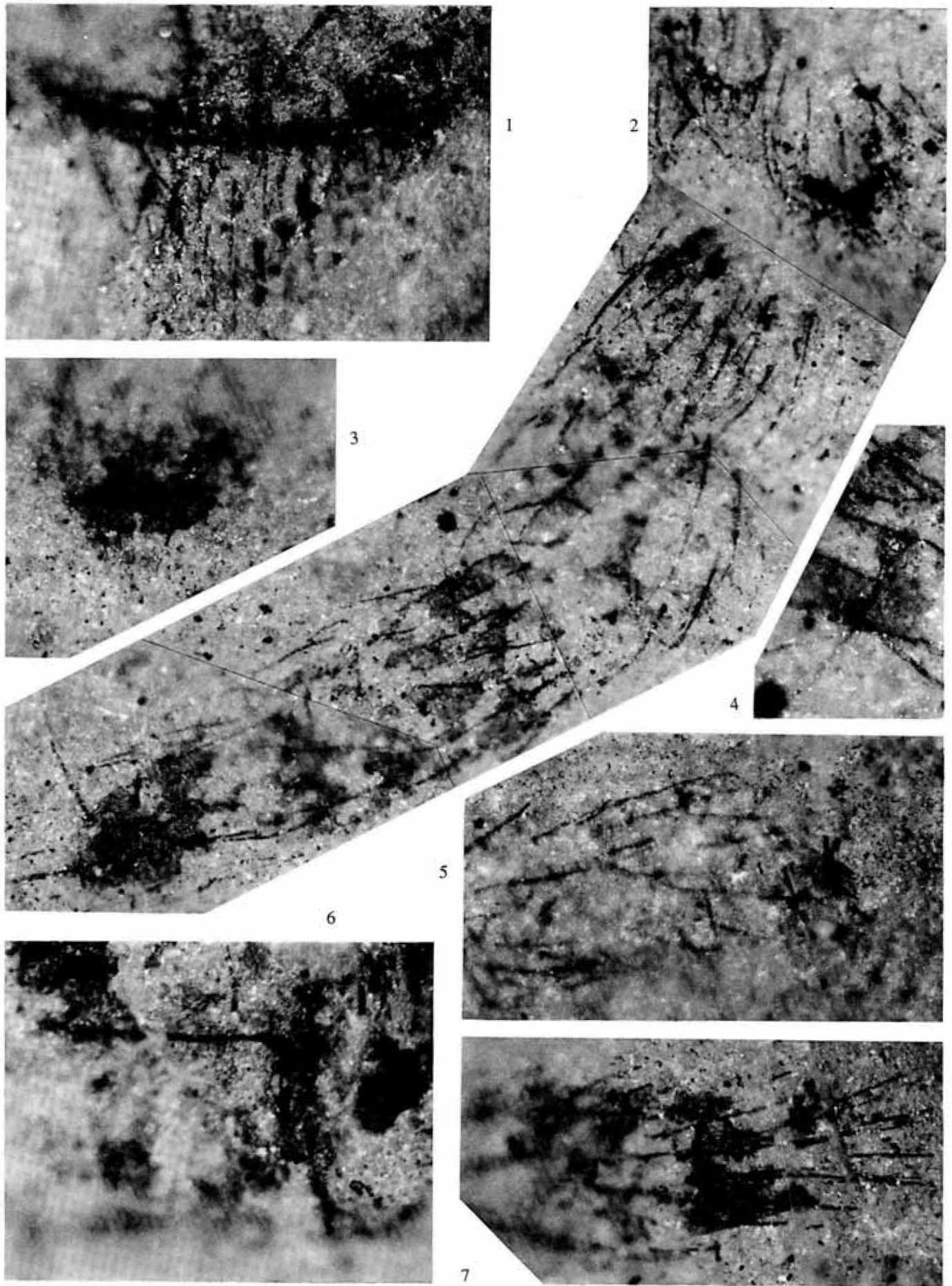
vegetation into the mud. Could *Rosamygale* spiderlings have ballooned? It is thought that mygalomorphs balloon less commonly than araneomorphs not only because of differences in phenology and behaviour but also because of the larger size of most mygalomorph species compared to araneomorphs which balloon regularly. This question was addressed by Coyle *et al.* (1985), who measured the masses and volumes of the ballooning mygalomorphs *Sphodros* and *Ummidia* in comparison with ballooning araneomorphs and the non-ballooning mygalomorph *Antrodiaetus*. They found that whereas the frequency distribution of the ballooning spiderlings was strongly skewed towards those with lighter mass, heavier spiders, up to 6 mg, were also found ballooning. Using the method of volume estimation described in Coyle *et al.* (1985) (volume of a cylinder of body length and diameter carapace width), the *Rosamygale* specimens fall between 1.9 and 27.4 mm³. Using the regression results in Greenstone *et al.* (1985), the estimated masses of the *Rosamygale* specimens would be between about 2 mg and (by extrapolation) 32 mg. However, the masses of the mygalomorphs measured by Coyle *et al.* (1985) were about 35% less than the masses estimated from the regression graph of Greenstone *et al.* (1985). If such were the case in *Rosamygale*, then their masses would have been between about 1.4 and 20.8 mg. Notwithstanding the large mass at one end of this range, it falls within the observed range of mass of ballooning spiders: using sticky traps, Greenstone *et al.* (1987) found that the majority of aeronauts weighed between 0.2 and 2 mg but that the observed range was 0.2 to 25.5 mg. In another study, Dean and Sterling (1985) recorded spiders over 15 mm in length ballooning in Texas. Therefore, it is possible that *Rosamygale* used walking, rappelling, and/or ballooning for dispersal, although there is no evidence that the fossil spider ballooned.

After death in the water, it is likely that terrestrial animals like the spiders and insects would have floated on the surface of the water for some time. Some carcasses were trapped by the mucilage surrounding the insect eggs (Pl. 1, fig. 4). When the water underwent partial desiccation, the bodies of the animals became stuck in the muddy bottom. Subsequently, an influx of detrital mud covered the carcasses; this rapid sedimentation ensured exceptionally good preservation of the fossils.

The spiders are preserved as brown organic cuticle flattened by sediment compaction in most cases. Pyrite occurs in some specimens (Pl. 1, figs 1, 3), which suggests reducing conditions. A peculiarity of a few of the specimens (e.g. Pl. 1, figs 1, 3) is the three-dimensional preservation of the abdomen cast in calcium phosphate. Spider abdomens are covered only in thin cuticle to enable distension, and they are liable to burst even due to changes in osmotic properties of the medium. They are unlikely to be preserved three-dimensionally unless mineralization is rapid. Also, phosphate is a rare casting material in invertebrates. Though phosphate is present in organic tissues, when liberated it is swiftly recycled by other organisms. However, because of the exceptional taphonomic conditions present in the Grès à meules, rapid phosphatization could occur. Phosphatization requires an oxygen-depleted environment and abundant organic matter (Prévôt and Lucas 1990). The microbial film would have sealed the phosphates being released by the decay of the organic matter in the spiders' abdomens, preventing its re-use by other organisms. Acidic conditions produced by decaying organic matter would have released free calcium which combined

EXPLANATION OF PLATE 6

Figs 1–7. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR8; counterpart; anal tubercle (see Pl. 2, fig. 3), $\times 200$. 2, AR8; part; spinnerets of left of specimen (see Pl. 2, fig. 2), ALS (top left), PMS (top right), and PLS; note two segments in basal half of PLS revealed by change in direction of setae, and distribution of spigots (setae with bulbous bases, see fig. 4) especially at distal ends of spinnerets, lateral to left, $\times 200$. 3, AR8; part; anal tubercle (see Pl. 2, fig. 2), $\times 200$. 4, AR8; part; spigot from proximolateral side of distal segment of PLS (see fig. 2), note bulbous base, collar, and setiform hair projecting at high angle to normal setae, lateral down, distal to right, $\times 400$. 5, AR5; counterpart; distal tarsus with pectinate paired claw, $\times 200$. 6, AR8; counterpart, coxa of fourth leg on right of specimen (see Pl. 2, fig. 3), proximal to left, anterior to top, note costa coxalis terminating (on right) in anteroinferior articulation of coxa–trochanter joint, $\times 200$. 7, AR8; counterpart; distal end of PLS of right of specimen (see Pl. 2, fig. 3); compare with part (fig. 2), $\times 200$.



with phosphate to form apatite. Once the phosphatic nodule had formed, it would have prevented flattening of the abdomen during sediment compaction.

MATERIAL AND METHODS

Of thirteen specimens available for study, numbered AR1–12 and PC14, three proved not to be spiders: AR3 is an insect, and AR6 and AR9 are insufficiently preserved for certain identification. The ten spider fossils are preserved as small pieces of cuticle on and just within the fine clayrock. Mainly setae and spines are preserved, which provide an outline of the legs and body, and also of other sclerotized organs such as the chelicerae and parts of the carapace and abdomen. Splitting of the rock has resulted in part of each specimen being preserved on one slab, and part on another. These are termed part and counterpart for convenience, but do not correspond to dorsal and ventral, which are commonly indistinguishable. Comparison of part and counterpart reveals that most of the cuticle is preserved on one slab or the other (compare Pl. 2, figs 2–3 and Pl. 6, figs 2, 7). In addition, a little pyrite is present, and the abdomens and parts of the prosomae of two specimens are infilled with calcium phosphate (Pl. 1, figs 1, 3). Apart from the mineralization, the style of preservation is strongly reminiscent of that of the Lower Cretaceous spiders described from the Sierra de Montsech, Spain (Selden 1989, 1990). Similar methods of study to those used for the Montsech spiders were employed: examination and photography under alcohol at low magnification (less than $\times 200$ on the plates), and oil immersion reflected light microscopy for higher magnification ($\times 200$ or greater on the plates). Drawings were made from the photographs.

Abbreviations used in the Text-figures

ab	abdomen	p	palp
ALS	anterior lateral spinneret(s)	pa	patella
an tu	anal tubercle	PLS	posterior lateral spinneret(s)
ar	articulation	PMS	posterior median spinneret(s)
ch	chelicera	rast	rastellum
cx	coxa	sc	sclerite
f	fovea	sp	spine
fe	femur	st	sternum
la	labium	ta	tarsus
lyr	lyriform organ	ti	tibia
mt	metatarsus	tr	trochanter
mx	maxilla		

MORPHOLOGICAL INTERPRETATION

The reconstruction (Text-fig. 1) is based on morphological details present in the best-preserved, type series of specimens. In addition, information from living hexathelid spiders (e.g. those depicted in Forster and Wilton 1968) was taken into consideration where necessary.

The specimens range up to 6.8 mm in body length (AR1, including chelicerae); some of the best-preserved specimens, AR8 and AR12, are only 2.8 mm long (including chelicerae and anal tubercle). These small specimens are considered to be juvenile on account of the large anal tubercle, widely separated spinnerets (relative to the size of the abdomen), and the lack of spinose armature on the legs. Their palps are well preserved but show no signs of adult male modification. The palps of larger specimens AR1 and AR11, however, appear to end abruptly. This may be due to different preservation of male palps (see below).

The carapace is poorly preserved, only the cephalic lobe and anterior parts being visible in some specimens. The radial arrangement of the coxae suggests that the carapace was broadly oval to subcircular in life. Some unsculptured cuticle of the anterior part of the carapace is present in AR11. The cephalic area is marked by curved sulci which diverge anteriorly, together forming a parabola. AR8 and AR11 show a distinct, procurved line in the position which would be occupied by the fovea (Pl. 1, fig. 1; Pl. 2, fig. 2; Text-figs 3–4). These are not deep, and merge gradually into lines running

towards the anterolateral corners of the carapace. On this evidence, the fovea is reconstructed as transverse and procurved. Longitudinal cracks in AR11 suggest that the cephalic area was raised in life, but not strongly. The ocular region is preserved as a small patch of dark cuticle between the bases of the chelicerae (Pl. 1, fig. 1; Pl. 4, fig. 2). Some specimens show evidence of eyes (AR5, AR11, AR12), from which it is deduced that probably eight were present in two recurved rows. The darkness of the cuticle on the ocular area, which is noticeable even in specimens which lack cuticle of the remainder of the carapace, suggests it was thicker, and possibly raised, in life.

The outline of the sternum is well preserved in a number of specimens (Pl. 1, figs. 1, 3; Pl. 2, fig. 3; Pl. 3, figs 2-3; Pl. 4, fig. 2). It is approximately subcircular, but with a recurved anterior border which accommodates the broad labium (seen in AR1, Pl. 3, figs 2-3). The posterior of the sternum is produced slightly (but does not project between the fourth coxae), giving the whole plate a heart-shaped appearance. At each place where a coxa abuts the sternum, the sternal edge is slightly straightened, giving a slight scalloped appearance. Sigilla cannot be definitely determined in any specimen.

The chelicera (Pl. 2, figs. 2, 4; Pl. 3, figs 1, 4; Pl. 4, figs 2-4) is oval in outline, and broadest distal to the midlength. The chelicerae diverge, but lack flat mesial faces adpressed to each other, which are common in many mygalomorphs. The orthognath fang arises from an anteroinferior position; it is gently curved and almost as long as the body of the chelicera. Small patches of dark cuticle alongside the fang indicate the presence of a row of small teeth. On AR1 and AR8 (Pl. 3, figs 1, 4), an area of dark triangular cuticle patches on the chelicera mesial to the fang base is interpreted as a small rastellum of short teeth. No rastellar lobe is apparent. AR8 also shows a long, gently sinuously curved bristle arising from the mesial face of the chelicera (Pl. 3, figs 2, 4).

The maxilla does not bear a lobe; it is commonly seen as a strong line of dark cuticle (Pl. 4, fig. 3), which suggests that cuspules were present in life. Plate 3, figure 4 shows a row of long bristles arising from the maxilla. The remainder of the palp in small specimens is a typical juvenile palp; patella, tibia, and tarsus are well preserved in a number of specimens. The palp tarsus bears a single claw which appears to be non-pectinate (Pl. 5, fig. 2). In AR8, the palp patella shows a strong, curved spine on the inferior/mesial surface (Pl. 5, fig. 4; Text-fig. 6B); this is very similar to the curved spine present on the tibia of leg 1 of males of many mygalomorphs, used as a clasper during mating. The palps of AR1 and AR11 are not well preserved in these specimens, even though the other appendages are. In the palps of AR1 and AR11 (Pl. 1, figs 1, 3; Pl. 3, figs 2-3), a long podomere (i.e. the femur or the tibia) has an oddly shaped, short piece of the next distal podomere attached, and no more is preserved. It seems strange that the remainder of the palp is not preserved; possibly these are adult males, and the distal parts of the palp were turned laterally so that they are now obscured by the first walking legs; this is supported by the preservation of AR11 (Pl. 1, figs 1, 4; Text-fig. 2). The stiff bristles on the walking legs of the larger specimens (see below) suggest these are males; they could be subadult males, which have swollen but not erupted palpal tarsi, and there is evidence of penultimate males of *Microhexura* wandering or ballooning (Coyle 1981).

The walking legs appear to be approximately equal in length, although the distal podomeres of legs 3 and 4 are not well preserved in any specimen. They are about two-thirds of the length of the body. Leg 1 is slightly shorter than leg 2 in AR12 (Pl. 4, fig. 2, an immature), tarsus 1 being shorter than metatarsus 1, whereas these podomeres are nearly equal in length in leg 2. The podomeres show few modifications, being typical in morphology for the suborder (see, for example, the metatarsus-tarsus joint in Pl. 5, fig. 3). The coxae are well preserved and show a distinct costa coxalis which runs along the anteroinferior surface, terminating in the anteroinferior coxa-trochanter articulation (Pl. 2, fig. 3; Pl. 6, fig. 6). The trochanter shows a groove running anteroposteriorly along the inferior surface. On AR11, this groove appears closer to the distal border of the podomere on more anterior trochanters. The legs are clothed in setae, which are arranged in rows on the femora of larger specimens (Pl. 3, fig. 3). Long, thin, curved bristles, arising at a high angle from the podomere, are numerous on post-trochanteral podomeres of the walking legs, particularly of larger specimens (Pl. 3, figs 2-3; Pl. 4, fig. 2). No definite trichobothria have been observed (it is assumed that trichobothria were present), but some of the setal bases bear a

great similarity to trichobothrial bases (Pl. 1, fig. 2). Some thicker bristles or spines can be seen on the palp patella of AR8 (Pl. 5, fig. 4). Metatarsus 1 of AR12 (Pl. 4, figs 1–2) is emarginated laterally and bears a distinct thorn.

The outline of the abdomen is preserved in most specimens. It is oval in outline, broadest at midlength, and is rather broader in larger specimens presumably due to their greater maturity. The abdomen is clothed in setae. These appear fine in smaller specimens, but relatively shorter in larger ones. The setae arise from small, slightly recurved transverse cuesta-like grooves, seen in internal mould in AR11. AR12 (Pl. 4, fig. 2) shows two pairs of slightly larger setae on the dark patch of cuticle (see later). A patch of dark cuticle covers the anteromedian third of the abdomen. The dark cuticle is oval in shape, but irregular and is not clearly defined at the edges; it is presumed to have been dorsal in life. In AR11 (Pl. 1, figs 1, 3), the abdomen of which is preserved primarily as an internal mould, there are no breaks of slope which would clearly indicate sclerites. Darker colouration in fossil arthropods results from a thicker cuticle (which is commonly correlated with sclerotization and pigmentation in life), for example the *Gilboa* specimens (Selden *et al.* 1991) and the Montsech spiders (Selden 1990). Mygalomorph abdomens usually bear a thin cuticle, though some (e.g. Atypidae, Mecicobothriidae, Microstigmatidae) have one or more dorsal sclerites. When present, pigmentation in living mygalomorph abdomens is not cuticular. So, it is considered that the dark area of cuticle in *Rosamygale* represents sclerotization in which true tergites are not clearly defined. The larger specimens (AR1, Pl. 3, figs 2–3; AR11, Pl. 1, figs 1, 3) do not show the dark area clearly, so it is possible that the sclerotization was present only in early juveniles.

The small specimen AR8 shows the juvenile arrangement of the spinnerets and anal tubercle. In this specimen, the anal tubercle is large, and on either side arise long PLS (Pl. 2, figs 2–3). The PLS is two-thirds the length of the abdomen. The distalmost segment of the PLS is digitiform, half the length of the whole appendage, and there is no evidence of pseudosegmentation. Consideration of the trends of the preserved setae indicates that two segments, approximately equal in length, are probably present proximal to the distalmost segment (Pl. 5, fig. 5; Pl. 6, fig. 2). Thus, it is probable that three segments are present. Anterior to the base of the PLS are two pairs of short spinnerets, the ALS and PMS (Pl. 2, figs 2–3; Pl. 5, fig. 5; Pl. 6, fig. 2). The ALS appear to be very slightly smaller than the PMS; there is no evidence of more than one segment in each of these spinnerets. The anal tubercle (Pl. 6, figs 1–2) is visible in some larger specimens (AR11), but is much smaller in relation to the size of the abdomen than in the juvenile. On all spinnerets, some setae can be seen by their bulbous bases to be modified into silk-producing spigots; these occur distally on ALS and PMS, and distally and laterally along the length of the PLS (Pl. 5, fig. 5; Pl. 6, figs 2, 4, 7).

DISCUSSION

Phylogeny

Raven (1985) produced an important revision of the systematics of the Mygalomorphae, dividing the infraorder initially into two microorders: Tuberculotae and Fornicephalae. He placed Antrodiaetidae, Atypidae, Migidae, Actinopodidae, Ctenizidae, Idiopidae, and Cyrtaucheniidae in Fornicephalae, and all other families in Tuberculotae. Eskov and Zonshtein (1990) re-examined relationships within the Mygalomorphae based on new information from Cretaceous mygalomorphs and a critical assessment of Raven's (1985) character analysis. They recognized two superfamilies within the infraorder Mygalomorphae: Atypoidea (including Atypidae, Mecicobothriidae, and Antrodiaetidae) and Theraphosoidea. At a crude level, the major difference between these schemes lies in Eskov and Zonshtein's allying of Mecicobothriidae with Antrodiaetidae and Atypidae, and, in contrast, their placement of Cyrtaucheniidae near to Hexathelidae and Dipluridae. Our find of a new, older mygalomorph in the Triassic does not have great bearing on these phylogenetic schemes. However, being twice as old as any previously described mygalomorph, the position of *Rosamygale* in the phylogenetic scheme of Mygalomorphae is interesting. The characters of *Rosamygale* which are important in phylogenetic discussion are: the six functional spinnerets, including single-segmented ALS and PMS, and three-segmented PLS with a digitiform

distal segment; the transverse, procurved fovea; lack of maxillary lobes; the wide labium; the large, irregular, dorsal abdominal sclerite; the few, broad teeth constituting a cheliceral rastellum; the tarsi lacking pseudosegmentation, claw tufts and scopulae, with three claws not on a lobe, and pectinate paired claws with numerous teeth.

Presence of six spinnerets is a primitive feature within the mygalomorphs. The ALS are lost in many groups; their retention in Atypidae, Antrodiaetidae, Hexathelidae, Mecicobothriidae, and Microstigmatidae is considered a plesiomorphic condition (Raven 1985). While acknowledging the plesiomorphic nature of ALS retention, Eskov and Zonshtein (1990) used the possession of four and six spinnerets to define theraphosoids and atypoids respectively. However, these authors acknowledged an independent reduction in some atypoids and the retention of six spinnerets by some archaic theraphosoids. The presence of three segments in the PLS was considered plesiomorphic by Raven (1985). Eskov and Zonshtein (1990), on the other hand, proposed that the four-segmented (excluding pseudosegments) PLS possessed by some members of the Mecicobothriidae and Atypidae was the plesiomorphic condition, and therefore that the three-segmented PLS was separately developed by all Theraphosoidea, Antrodiaetidae, and the majority of atypids and mecicobothriids. The digitiform distal segment of the PLS was regarded as plesiomorphic by Raven (1985), and this conclusion was not contradicted by Eskov and Zonshtein (1990). So, we consider that the characters of the spinnerets in *Rosamygale* are in the most plesiomorphic state for the Mygalomorphae, the only possible exception being the three-segmented nature of the PLS.

The shape of the fovea has been used to define a variety of groups within the Mygalomorphae; among those families with six spinnerets, a transverse fovea is found in Atypidae, Hexathelidae, and Microstigmatidae. Eskov and Zonshtein (1990) discussed foveal shape, concluding that, in general, their Atypoidea possess a longitudinal fovea, and the Theraphosoidea a transverse one. Foveae contradicting this generality (e.g. atypids) were considered to resemble the pit found in *Liphistius*, and therefore plesiomorphic. The fovea in *Rosamygale* compares with the Theraphosoidea of Eskov and Zonshtein (1990) but, because of the poor recognition of the fovea in the fossils, it could be a transverse pit.

Atypids bear characteristically elongate maxillary lobes, which Gertsch and Platnick (1980) and Raven (1985) proposed as an autapomorphy for the family. Eskov and Zonshtein (1990) argued that similarly elongated maxillary lobes of some mecicobothriids (considered by Raven to be of different origin from those of the atypids) is a synapomorphy between the Mecicobothriidae and the Atypidae. The absence of such lobes in *Rosamygale* indicates a difference between the fossil genus and these extant families. A wide labium is generally regarded as plesiomorphic.

One or more dorsal abdominal sclerites are known in a number of mygalomorph families (Atypidae, Mecicobothriidae, Microstigmatidae), and have traditionally been considered as homologues of liphistiomorph tergites, and their presence thus plesiomorphic within Mygalomorphae. Eskov and Zonshtein (1990) used the presence of abdominal sclerites as a synapomorphy for their Atypoidea, the only occurrence of such sclerites in their Theraphosoidea being in the diminutive microstigmatids. Certainly, abdominal sclerotization is a feature associated with miniaturized body size in a number of spider families, such as the Oonopidae and Tetrablemmidae. Though small for a mygalomorph, *Rosamygale* is not as small as the microstigmatids, adult males of which range down from 3 mm to less than 1 mm in body length (Raven and Platnick 1981; Platnick and Forster 1982). Nevertheless, the abdominal sclerotization may be related to the small size of the fossil form, and it is possible that it is lost or greatly reduced in adults. The abdominal sclerotization of *Rosamygale* is not very useful as an indicator of affinity, because it could be a plesiomorphic character, a feature of small body size, or both.

The rastellum consists of a group of thorns at the anteromesial corner of the chelicera, and ranges from absent to a distinct lobe bearing long spines. Raven (1986) pointed out that the rastellum varies greatly, even within a family; it is correlated with a burrowing habit (Eskov and Zonshtein 1990). Therefore, the poorly developed rastellum of *Rosamygale* is an indicator of the mode of life of the spider (see below) rather than its affinities. Nevertheless, *Rosamygale* differs from groups with characteristically burrowing habits, such as the Atypidae and Antrodiaetidae, in this respect.

TABLE 1. Mid-Tiassic stratigraphy of the northern Vosges, France. *Rosamygale grauvogeli* gen. et sp. nov. occurs in the Grès à meules, the lower part of the Grès à Voltzia of the Buntsandstein Supérieur.

STRATIGRAPHY OF THE BUNTSANDSTEIN IN THE NORTHERN VOSGES (FRANCE)										
MEMBERS AND FORMATIONS				Thickness (m)	Palaeo- environ- ment	Palaeontology				
French nomenclature		German nomenclature				Plants	Inverte- brates	Verte- brates	Traces	
MUSCHELKALK INF.	Niveaux dolomitiques supérieurs	UNT. MUSCHELKALK	Mittlere und obere Abteilung der Wellenkalkgruppe	15-20	shallow marine		•	•	••	
	Couches à Myacites		Myacitenbänke	30			•••	•	••	
	Grès coquillier		Muschelsandstein	20-30			•••	•	••	
BUNTSANDSTEIN SUPERIEUR	GRES A VOLTZIA	OBERER BUNTSANDSTEIN	VOLTZIEN- SANDSTEIN	Lettenregion	7-8	deltaic to marine	•	•••	•	•••
				Werkstein	10-12	coastal fluvial to deltaic	•••	•••	•••	••
	Couches intermédiaires supérieures		Obere Zwischenschichten	15-25	inland fluvial	•	•		•	
	Couches intermédiaires inférieures		Untere Zwischenschichten	30						
	BUNTSANDSTEIN MOYEN		Zone-limite violette	MITTLERER BUNTSANDSTEIN	Violette Grenzzone		4-5	palaeosol	•	
Conglomérat principal		Haupt konglomerat			20	inland fluvial				
Grès vosgien supérieur		Oberer Vogesensandstein			150-200			•		•
Grès vosgien inférieur		Unterer Vogesensandstein			150-200					
BUNTSANDST. INFÉRIEUR	Grès d'Annweiler	UNTERER BUNTSANDST.	Annweiler Sandstein		50-60	fluvial and playa lake				•

PALAEOECOLOGY

Evidence from the sediments and fossils points to a deltaic sedimentary environment (Gall 1971, 1983). The sandstone facies corresponds to point bars deposited in strongly sinuous channels; the clay lenses represent the settling of fine material in brackish ponds; the calcareous sandstone results from brief incursions of sea water during storms. The palaeogeographical position for the localities, in the subtropics near the eastern edge of Pangaea, together with the red-beds and the xeromorphic nature of the land flora (Gall 1983), suggest a semi-arid climate in the region. However, the low-

Pseudosegmented tarsi are present, normally in males only, in a number of mygalomorph taxa (Ischnothelinae, Diplurinae, Atypidae, Antrodiaetidae, and some Pycnothelinae, Theraphosidae, and Barychelidae (Raven 1985)). Therefore, the absence of pseudosegmentation in *Rosamygale* suggests it does not belong with these taxa. The tarsi of *Rosamygale* lack claw tufts and scopulae. Claw tufts are known in Theraphosidae, Barychelidae, and a few other, isolated genera (Raven 1985, 1986), and scopulae are present in many groups, including Theraphosidae, Barychelidae, and Nemesiidae. The combination of claw tufts and scopulae was considered as an autapomorphy of the Theraphosidae by Raven (1985). In general, scopulae are thicker and more extensive on the anterior legs than on the posterior, and are generally developed to aid locomotion on smooth surfaces. The absence of these tarsal structures in *Rosamygale* indicates no close relationship with these taxa, the Crassitarsae of Raven (1985). The other tarsal characters of *Rosamygale*, three claws and numerous teeth on the paired claws, also indicate no close relationship with this group.

The discussion above indicates that most characters of *Rosamygale* are in the plesiomorphic state for the Mygalomorphae. Many characters separate the fossil genus from Raven's (1985) Rastelloidina and Crassitarsae (essentially Eskov and Zonshtein's (1990) Ctenizoidina and Theraphosoidina). Sufficient apomorphies in the Atypidae and Antrodiaetidae (e.g. elongated maxillary lobes, rastellum) distance *Rosamygale* from these families, and the derived nature of the PLS distinguish Mecicobothriidae and Microstigmatidae from the fossil genus. *Rosamygale* differs from the described Hexathelidae in the presence of abdominal sclerotization and a small rastellum. Additional features can be used to argue a relationship with the Hexathelidae, and the basal position of *Rosamygale* within Raven's (1985) Tuberculotae. The chelicerae of Atypidae and Antrodiaetidae are much larger in relation to the size of the carapace than in *Rosamygale*. The walking legs are nearly equal in length in *Rosamygale*, whereas legs 1 and 2 are shorter in the Fornicephalae (Raven 1985). Raven (pers. comm. 1990) has suggested that the general appearance of *Rosamygale* (Text-fig. 1) compares most closely with *Bymainiella* Raven, 1978 among living hexathelids. However, it differs from that genus in size (the largest known *Rosamygale* is about the same size as the smallest *Bymainiella*) and compares more closely in this respect with the Microstigmatidae (Raven and Platnick 1981) and the diplurid *Microhexura* (Coyle 1981).

We consider that *Rosamygale* is best placed in the Hexathelidae, differing from all other known members of that family by its possession of sclerotization dorsally on the abdomen (which may be a function of small size and lost in adulthood) and the small rastellum (which functions in digging).

Mode of life

The morphological features of *Rosamygale* discussed above, together with its geological and palaeoecological setting, give good indications of the mode of life of the spider. Mygalomorphs live primarily in warm climates at the present day, although the atypids *Atypus* and *Sphodros* inhabit the temperate palaeoarctic, and a few reach alpine habitats, for example the diplurid *Microhexura* occurs up to 2300 m elevation in the Pacific northwestern USA (Coyle 1981). Geological evidence (given above) points to a hot climate for the Vosges area in the Anisian, though the near-marine situation and evidence for periodic flooding and drying out suggests the area was humid for at least part of the year.

Many mygalomorphs are noted for their adaptations to arid habitats, being the dominant spiders in such habitats in Australia, and their adaptive strategies have been well documented by Main (1982, and references therein). Behavioural adaptations to reduce desiccation include living in a burrow, aestivation, and dispersal during wet seasons (see above). Morphological adaptations in mygalomorphs to reduce water loss include various cuticular specializations of the abdomen (?wax-secreting disks, reduced pilosity, spiny sclerotized cuticle), and larger body size (Main 1982). Such morphological adaptations do not occur in *Rosamygale*, which may, nevertheless, have used behaviour for drought avoidance. Indeed, the presence of a small rastellum indicates the digging ability of the fossil spider.

Modern hexathelids inhabit wet forest areas (Raven 1978; Main 1981): a few burrow, but most weave a silken tube under stones, logs, bark, litter, and in cracks in the ground. Long PLS are

characteristic of mygalomorphs which construct broad platforms outside their funnel webs for prey capture, and in the mecicobothriids and diplurids the PLS are enormously elongated for this purpose (Gertsch and Platnick 1979; Coyle 1984, 1990). Discussion under TAPHONOMY, above, suggested that *Rosamygale* may have lived in the soft, sandy banks of watercourses, or beneath litter thereon (see reconstruction, fig. 9 in Gall (1985), but note that it is unlikely that the spider climbed trees, except perhaps during dispersal). Like other mygalomorphs, *Rosamygale* probably lived most of its life in its nest, venturing abroad as a juvenile seeking a new nest site, or as a mature or subadult male wandering in search of a mate. The abundant insects (Gall 1983) would have provided a food source for *Rosamygale*. Most of the described forms have aquatic larvae; presumably terrestrial insects were also present; nevertheless, it is conceivable that reliable food sources were present only in humid periods, and that *Rosamygale* aestivated during droughts. Aestivation is common in mygalomorphs which inhabit seasonal habitats (Main 1982). The habitat of *Rosamygale* compares with that of some nemesiids, as described by Main (1981), which are restricted to damp habitats within semi-arid, seasonal climatic regimes.

Biogeography

Apart from the ballooning habit of spiderlings of some species, mygalomorphs are generally good subjects for the study of biogeography because of their sedentary habits (Pocock 1903). At present, hexathelid spiders range from eastern Australia and Tasmania, through New Zealand, to Chile, and one genus, *Macrothele*, occurs in West Africa, southern Europe, India, China, Malaysia, Burma, Vietnam, Japan, and Java (Raven 1985; Snazell and Allison 1989). The related mecicobothriids inhabit western North America and Argentina; the microstigmatids are found in South Africa, South America, and Panama; and the Dipluridae occur in tropical and subtropical regions, mainly southern (Raven 1985). It is not surprising, therefore, that Gondwanaland has been suggested as the original home of this group of mygalomorphs.

Main (1981) discussed the evolutionary biogeography of Australian mygalomorphs. She recognized three evolutionary phases of mygalomorph faunas: (1) ancient (i.e. Mesozoic, early Palaeogene) Gondwanan relicts; (2) less ancient, but autochthonous forms; and (3) Neogene and Pleistocene immigrants. Hexathelids belong to the first group, and this family was discussed in greater detail by Raven (1980). In his biogeographical discussion, Raven (1980) suggested that the ancestor of the family arose in East Antarctica in the early Jurassic, and the group radiated throughout Gondwanaland before it broke up. The presence of *Rosamygale* on the southern shore of the Zechstein Sea in the Middle Triassic indicates that hexathelids, including *Rosamygale*, were probably present throughout Pangaea prior to the break-up of the supercontinent. However, the centre of dispersal of the group is not clear.

Geological history

The only previously described Mesozoic mygalomorphs are a mecicobothriid, an atypid, and an antrodiaetid from the Cretaceous of the Soviet Union, described by Eskov and Zonshtein (1990). Although the diagrams of these specimens are clear, the photographs are poor and the descriptions minimal, so it is difficult to judge the evidence for the assignments of these fossils. However, the placements seem reasonable on the scant evidence presented, and the Cretaceous fossils are quite distinct from *Rosamygale*. Eskov and Zonshtein (1990) discussed the Mesozoic Mygalomorphae in relation to the meagre geological history of the order. Eskov (1984, 1987) had described araneomorphs from the Jurassic which, together with the diversity (i.e. three families) of Cretaceous mygalomorphs, Eskov and Zonshtein (1990) used as evidence for a short 'Age of Mygalomorphs' during the latter part of the early Cretaceous. During this time, they concluded, a range of atypoid mygalomorphs replaced the Jurassic araneomorphs, at least in central Asia. Later, in the Palaeogene, theraphosoids replaced atypoids as the dominant mygalomorphs in the fossil record, but Eskov and Zonshtein (1990) considered that the theraphosoids had been present at low diversity since the early Mesozoic. They linked the faunal changes to changes in flora and insects during the late early Cretaceous.

The fossil record of Mesozoic spiders is currently far too scanty to allow analysis of major events, as Eskov and Zonshtein (1990) attempted, although the evidence so far accumulated does support that of the insects, which indicates trivial extinction of taxa across the Cretaceous-Tertiary boundary. The currently known fossil record of spiders (Selden 1990) begins in the Devonian, with *Attercopus* Selden and Shear, 1991 as the sister taxon to all other spiders. Only liphistiomorphs were present in the Carboniferous (all supposed araneomorphs studied by P.A.S. have so far proved not to be spiders). The present find of a Triassic mygalomorph sits almost centrally within the longest gap (c. 100 Ma) in the spider fossil record, and lends support to the notion that mygalomorphs arose from liphistiomorphs and in turn gave rise to araneomorphs. If an 'Age of Mygalomorphs' existed, before the advent of the Araneomorphae, it would have occurred around this time.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757

Suborder OPISTHOTHELAEC Pocock, 1892

Infraorder MYGALOMORPHAE Pocock, 1892

Remarks. The presence of six spinnerets, posteriorly situated on the abdomen, the PLS consisting of three segments, and the paraxial chelicerae confirm that *Rosamygale* is a mygalomorph spider (for discussion of characters and relationships of spider suborders see Platnick and Gertsch (1976) and Raven (1985)).

Family HEXATHELIDAE (Simon, 1892)

Remarks. The subfamily Hexathelinae of the family Dipluridae (which is the sister-group of the Hexathelidae), was accorded familial status by Raven (1980). It is diagnosed principally by the presence of numerous labial cuspules. *Rosamygale* differs from typical hexathelids in possessing a group of blunt teeth forming a small rastellum on the chelicera, and the probable sclerotization of part of the dorsal surface of the abdomen. In having such sclerotization, *Rosamygale* resembles some of the related mecicobothriids and microstigmatids. The rastellum is an organ used for digging, and though characteristic of the Rastelloidina Raven, 1985, it also occurs in the Tuberculotae where it is not diagnostic. *Rosamygale* is included in this family for convenience and with these reservations; there is no doubt that it is a plesiomorphic tuberculote (*sensu* Raven 1985).

Genus ROSAMYGALE gen. nov.

Derivation of name. Latin *rosa*, a rose (ex Greek *rhodos*, red), from the delicate pink hue of the mineral infill of the abdomen of the specific holotype, reminiscent of the fine rosé wines of Alsace, and French (also obsolete genus name) *mygale*, a bird-eating spider.

Type and only known species. *Rosamygale grauvogeli* sp. nov.

Diagnosis. Hexathelid with six functional spinnerets, ALS and PMS single-segmented, PLS three-segmented; distal segment of PLS digitiform; fovea transverse, procurved; no maxillary lobes; large, irregular, dorsal abdominal sclerite present; cheliceral rastellum consisting of a few broad teeth; tarsi not pseudosegmented, without claw tufts or scopulae; three claws present, not on a lobe, pectinate paired claws with numerous teeth; labium wide.

Rosamygale grauvogeli sp. nov.

Plates 1-6; Text-figs 1-6

1971 *Araneida incertae sedis* Gall, p. 37, pl. 6, fig. 1.

Derivation of name. In honour of the collector of the Triassic spiders of the Grès à Voltzia, Louis Grauvogel.

Material. Holotype AR11; paratypes AR1, AR8, and AR12. Additional specimens: AR2, AR4, AR5, AR7, AR10 (part figured by Gall 1971, pl. 6, fig. 1; not available for this study, counterpart only seen), PC14. All specimens except AR2 consist of both part and counterpart. All are from the Grès à meules, which form the lower part of the Anisian Grès à Voltzia. Localities are as follows (details in Gall 1971): AR1, Adamswiller, Bas-Rhin; AR2, AR4, AR5, AR7, AR12, and PC14, Arzwiller, Moselle; AR10, AR11, Bust, Bas-Rhin; AR8, Vilsberg, Moselle. Specimens are deposited in the Grauvogel-Gall Collection, under the care of the Institut de Géologie, Université Louis Pasteur, Strasbourg.

Diagnosis. As for the genus.

Description. Body length up to 6.0 mm. Carapace subcircular, cuticle unsculptured. Fovea transverse, procurved. Eyes probably eight, on a raised lobe.

Sternum oval to subcircular, with recurved anterior edge, posterior projection (but not produced between fourth coxae), and scalloping adjacent to coxae on larger specimens. Labium wider than long, semicircular, possibly overlapping anterior edge of sternum.

Chelicerae robust, about one-quarter length of the carapace, and ovoid in shape (widest towards the distal). Orthognath fang arising from an anteroinferior position and following a gentle, scimitar-like curve to almost full length of body of chelicera. Row of small teeth present along inferior side of the cheliceral body. Small rastellum present, consisting of a few short spines distal and mesial to fang base, not on a lobe. Long bristle apparently arising from mesial side of chelicera.

Maxilla without a lobe, cuspules probably present, bristles present. Immature palp with single, ?non-pectinate claw; curved spine on patella. Legs not elongated, approximately equal in length (leg 1 slightly shorter than others), about two-thirds body length. Coxa with costa coxalis on inferoanterior surface, terminating distally in inferoanterior articulation of coxa-trochanter joint. Coxa 4 without liphistiomorph invaginations. Trochanter unnotched, with inferior groove on inferior surface. Legs covered with smooth setae, and spines on femur, patella and tibia at least. No claw tufts or scopulae. Metatarsus 1 with inferodistal spur. Tarsus with curved, pectinate paired claws, small median claw; without pseudosegmentation.

Abdomen oval, broadest at midlength. Cuticle with short setae arising from transverse wrinkles. Large, irregular sclerotized area occupying anteromedian third of dorsal surface. Six spinnerets, all with spigots. ALS and PMS single-segmented; ALS slightly smaller than PMS. PLS long, two-thirds length of abdomen. Distalmost segment of PLS digitiform, half length of spinneret, not pseudosegmented.

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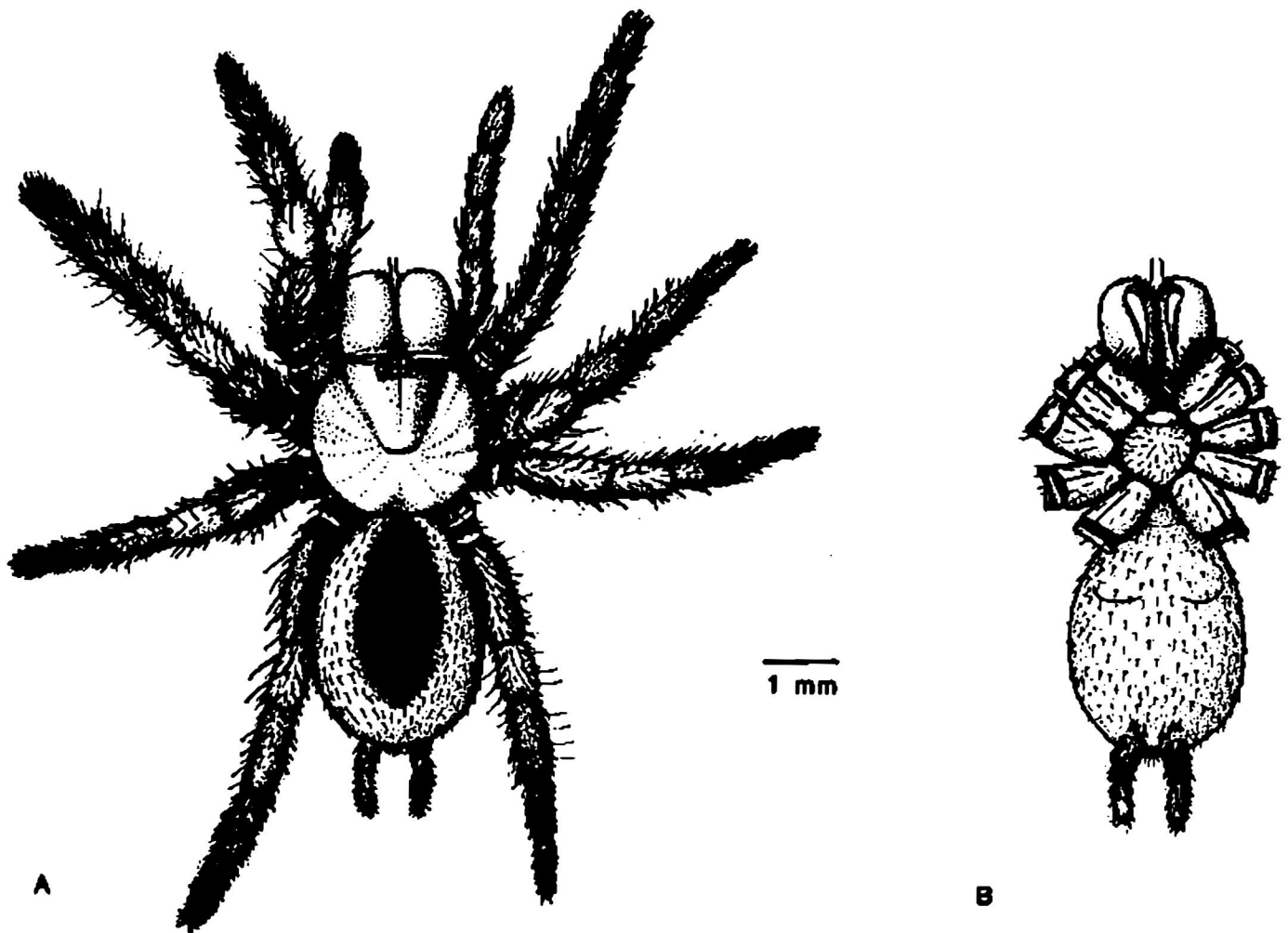
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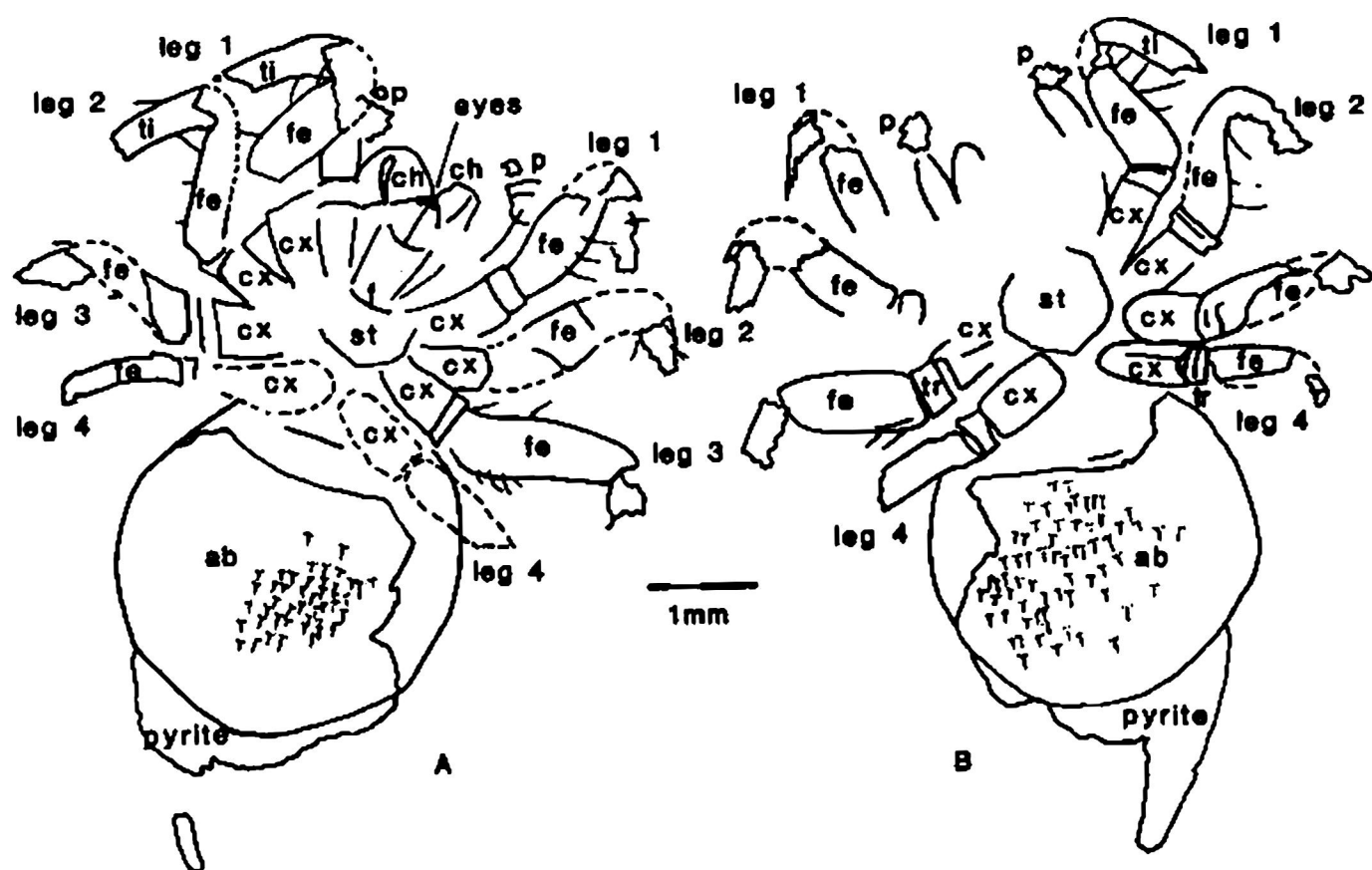


TEXT-FIG. 1. Reconstruction of juvenile *Rosamygale grauvogeli* gen. et sp. nov., based on type series and comparison with living hexathelids. A, dorsal. B, ventral.

lying, deltaic situation suggests that aridity was not severe locally. The climate was probably seasonal; the pools filling during the wet season and evaporating as the dry season approached. Eventually, the pools where the clay lenses were deposited became shallower and dried out completely. This is supported by the presence of desiccation cracks, reptile footprints, salt pseudomorphs and land plants in life position at the top of each clay lens. Also, moving upwards through each lens a transition from aquatic to terrestrial biota is observable (Gall 1983).

The excellent preservation of the terrestrial biota in the clay lens facies, the low energy of deposition, and the presence of *in situ* plant roots indicate that these organisms lived very near the water bodies. No evidence conflicts with the conclusions of Gall (1971, 1983) that the aquatic fauna lived and died *in situ* (i.e. it is autochthonous), and that the preserved terrestrial fossils crawled or fell from the adjacent terrestrial environment to their place of entombment. There is no evidence of drifting of the fossils by water currents. The kinds of plants and animals present, *Lingula's in situ* position, together with the impoverished species diversity, strongly suggest a brackish water community. The euryhaline fauna is typical of transitional environments such as lagoons, pools, and swamps between land and sea, and the dwarfed nature of the stenohaline marine forms supports this (Gall 1983). Such a fauna is adapted to fluctuating conditions of salinity, oxygenation, desiccation, etc. The composition of such restricted communities shows a striking continuity during the course of Earth history.

The spiders evidently inhabited the margins of the stagnant pools where a sparse vegetation grew,



TEXT-FIG. 2. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR11; holotype, part; explanatory drawing for Pl. 1, fig. 1. B, AR11; holotype, counterpart; explanatory drawing for Pl. 1, fig. 3.

grew, dominated by bushes of *Voltzia*, and reed beds formed by horsetails (*Schizoneura*, *Equisetites*). *Rosamygale grauvogeli* is the only known species of spider living in this Triassic landscape.

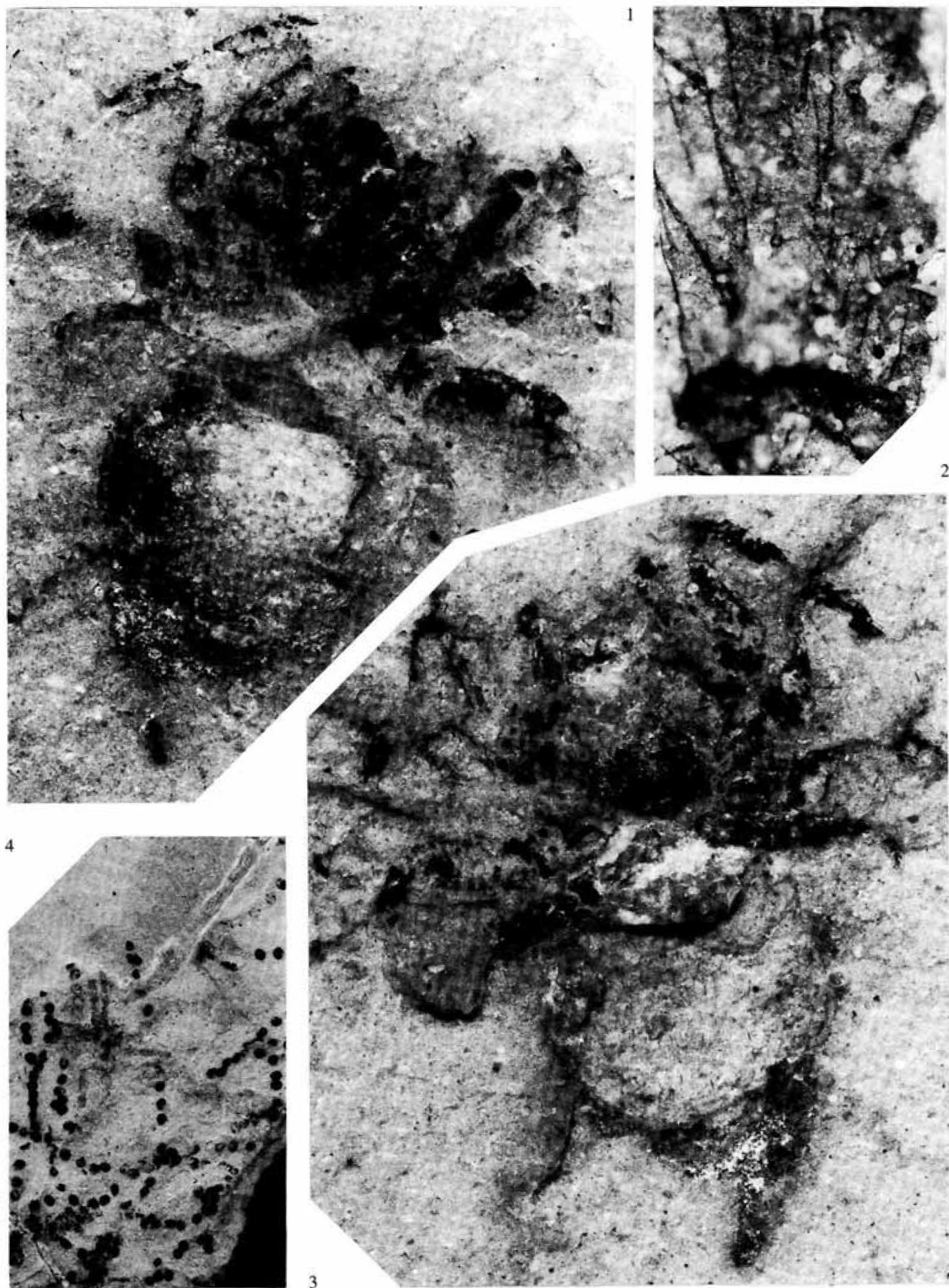
TAPHONOMY

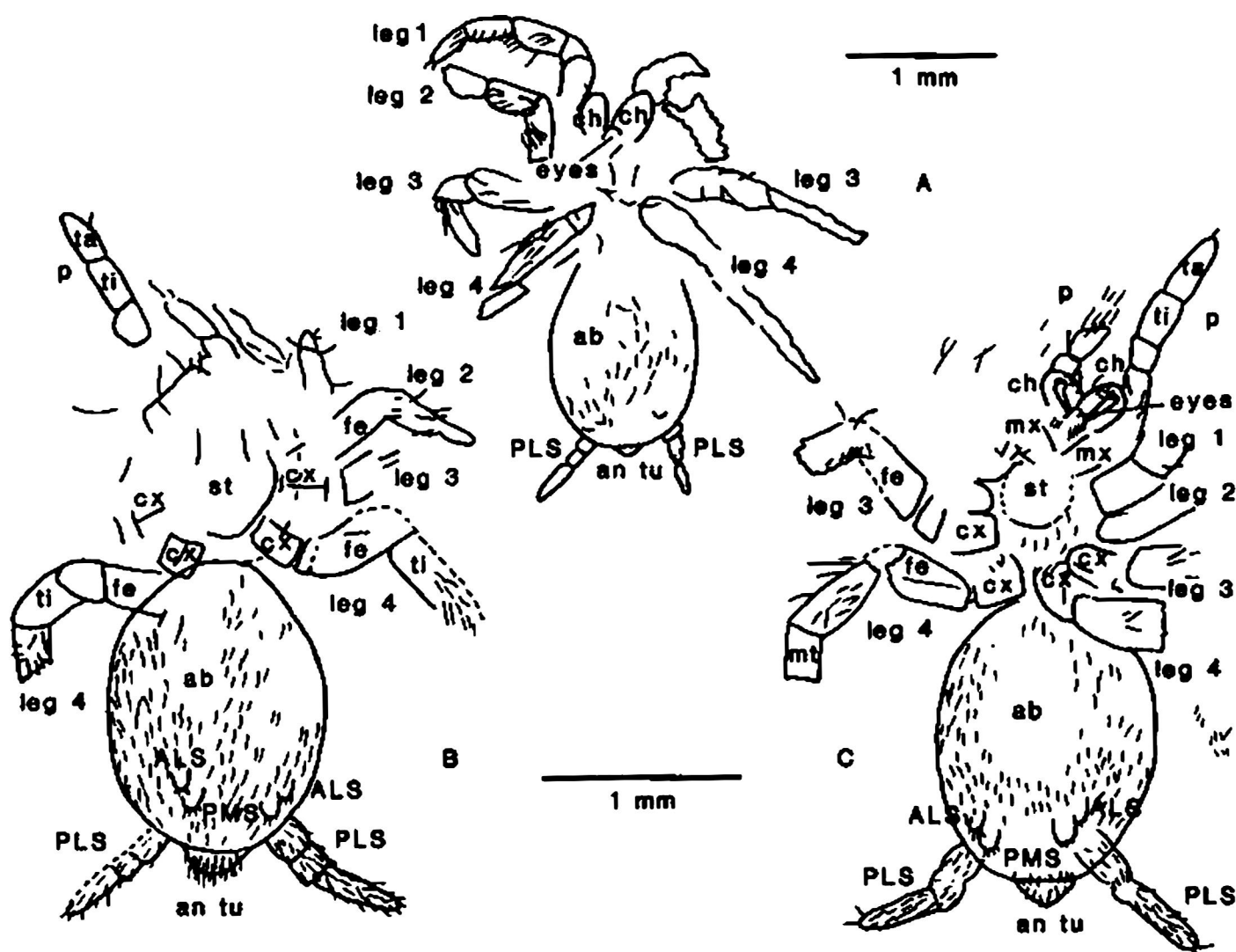
Drying-up of the pools led to death of the aquatic fauna. The abundance of estheriids is significant in that these crustaceans are adapted to swift completion of their life cycle in temporary water bodies. Regular high evaporation rates of the water bodies also favoured deoxygenation, consequent mass mortality of the aquatic fauna and the rapid proliferation of microbial films. Such films may have shielded the carcasses from scavenging activity and created, by production of mucus, a closed environment inhibiting the decomposition of organic material. Later, the deposition of a new detrital load (clay, silt) buried the microbial films and the organisms (Gall 1990).

There are three ways in which the spiders could have been transported to the site of deposition in the ephemeral pools: by water, land, or air. They may have been washed out of the watercourse

EXPLANATION OF PLATE 1

Figs 1–4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR11; holotype, part; see Text-fig. 2A for explanation, $\times 15$. 2, AR2; left femur, distal to top, showing various sizes of setae, note similarity of setal follicles to possible trichobothrial bases, $\times 200$. 3, AR11; holotype, counterpart; see Text-fig. 2B for explanation, $\times 15$. 4, PC14; poorly preserved specimen showing common association in rock with strings of insect eggs, *Monilipartus*, $\times 8$.





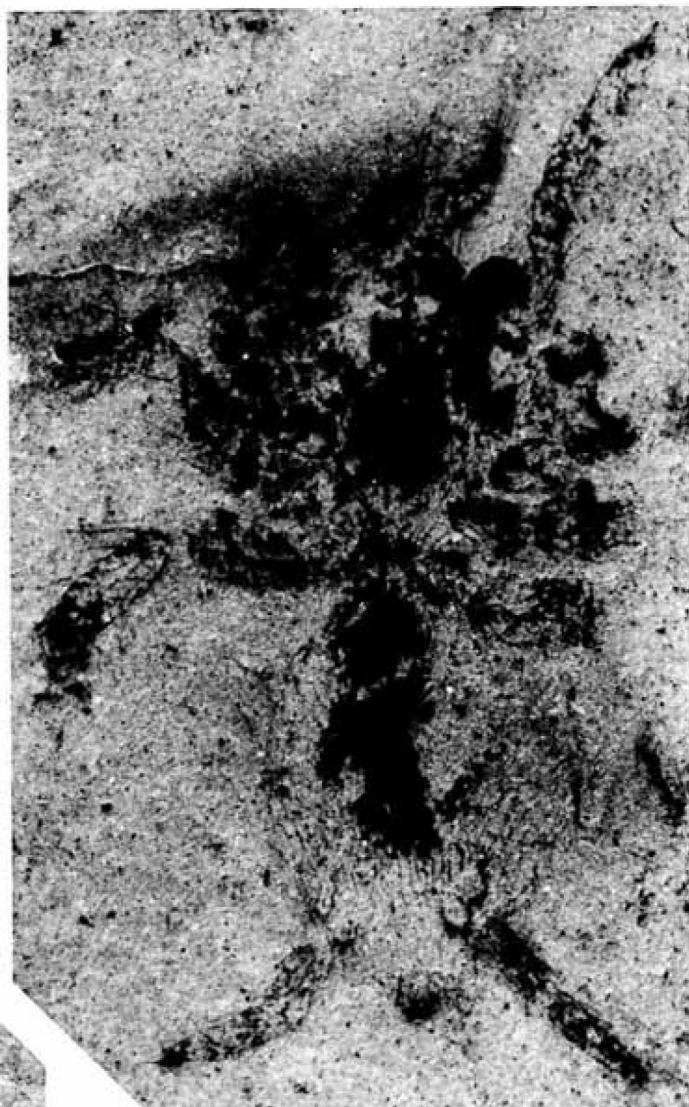
TEXT-FIG. 3. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR5; part; explanatory drawing for Pl. 2, fig. 1. B, AR8; paratype, part; explanatory drawing for Pl. 2, fig. 3. C, paratype, counterpart; AR8; explanatory drawing for Pl. 2, fig. 2.

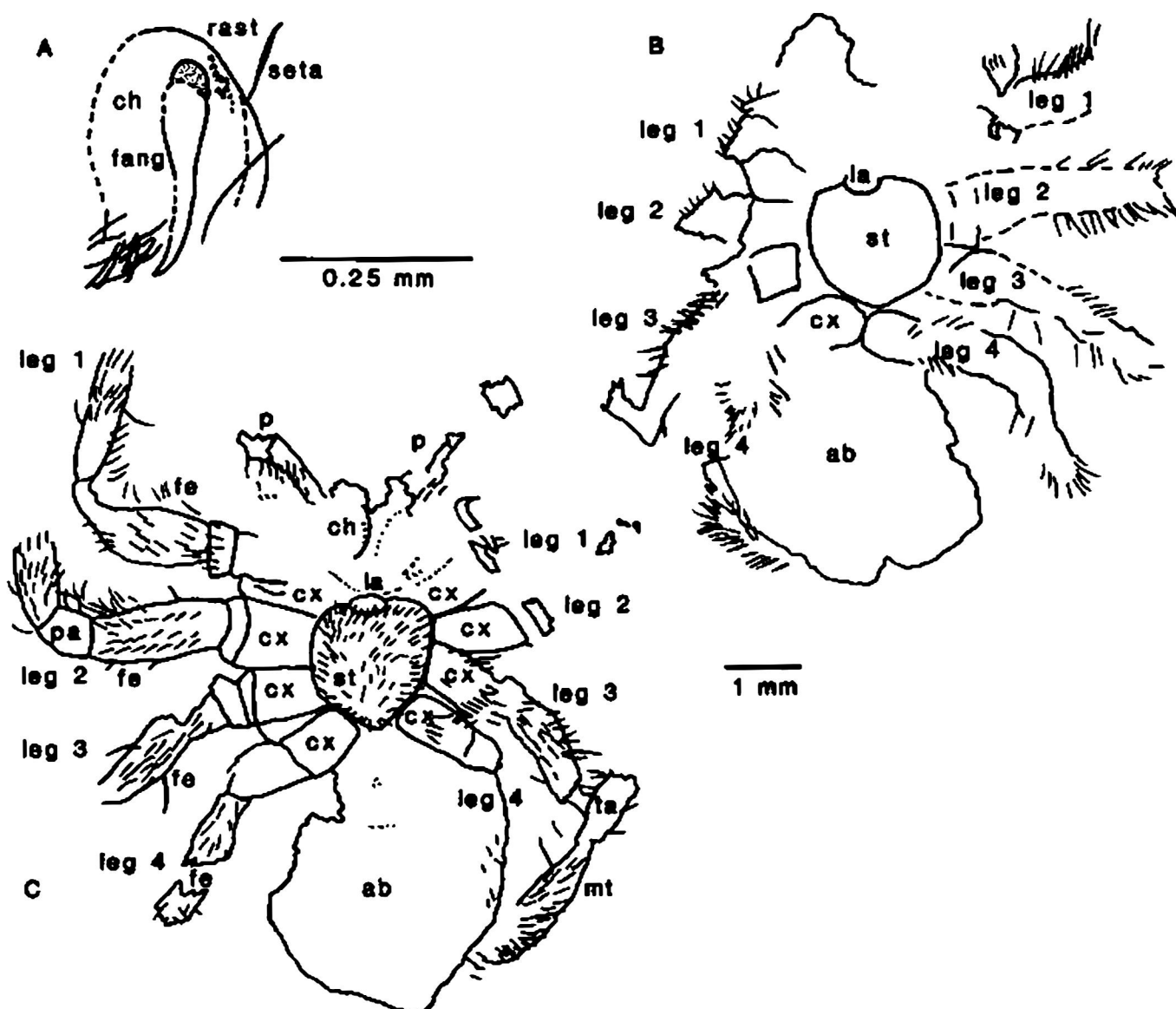
banks, perhaps still enfolded in the silk of their burrow linings or funnel webs; they may have been wandering free at the time and became trapped in the water, mud, or mucilage of the desiccating pools; they may have fallen from the air into the water or mud.

Water. Some of the fossils are preserved with their legs outstretched (Pls 2, 4), typical of spiders which have died in water, whereas the others (Pls 1, 3) show a death attitude with legs flexed around the body; none appears to be distorted by entanglement in silk. The energy of the water in the desiccating pools was low; although the spiders could have been washed in from some distance away and settled out in the lower energy environment, it is likely that there would be some evidence of silk adhering to the bodies, even if only as a distortion on the sediment surface. Extant

EXPLANATION OF PLATE 2

Figs 1-4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France; juvenile specimens. 1, AR5; part; see Text-fig. 3A for explanation, $\times 22$. 2, AR8; paratype, part; see Text-fig. 3B for explanation, $\times 30$. 3, AR8; paratype, counterpart; see Text-fig. 3C for explanation, $\times 30$. 4, AR10; counterpart to specimen figured in Gall (1971, pl. 6, fig. 1), $\times 20$.





TEXT-FIG. 4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. A, AR8; chelicera on left of part; explanatory drawing for Pl. 3, fig. 1. B, AR1; paratype, part; explanatory drawing for Pl. 3, fig. 2. C, AR1; paratype, counterpart; explanatory drawing for Pl. 3, fig. 3.

mygalomorphs living in semi-arid environments commonly construct intricate devices such as bathplug-like trap-doors, levees, and turrets to prevent the inundation of their burrows during flash floods (Main 1982). It seems unlikely that *Rosamygale* could have been washed in during flood periods, and remained intact with little decay, throughout a period of well-oxygenated conditions when an aquatic biota flourished in the water. Moreover, there is no evidence of any other organism now preserved in this facies having been washed in from very far away.

EXPLANATION OF PLATE 3

Figs 1–4. *Rosamygale grauvogeli* gen. et sp. nov. Triassic (Anisian) Grès à Voltzia; northern Vosges, France. 1, AR8; chelicera on left of part (see Pl. 2, fig. 2), mesial to right; see Text-fig. 4A for explanation, $\times 200$. 2, AR1; paratype, counterpart; see Text-fig. 4C for explanation, $\times 11$. 3, AR1; paratype, part; see Text-fig. 4B for explanation, $\times 11$. 4, AR8; chelicera on right of part (see Pl. 2, fig. 2), mesial to left, note patch of triangular teeth mesial to base of fang and part of long setae (both at top left), maxillary setae at bottom, $\times 200$.

